TREE GROWTH IN A MOIST TROPICAL FOREST OF PUERTO RICO

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INTRODUCTION

Information on growth rates, both for individual trees and for forest stands, is vital to forest planning and management. Such information is needed for a variety of sites and stand conditions in the moist tropical forests of the western hemisphere. In this paper, growth rates for individual trees are reported for two secondary stands and one mature stand in the Caribbean National Forest in Puerto Rico. Estimates are based on long-term measurements, taken in 1957 and again in 1975, on more than 2,000 individuals of 18 species. In addition, the variability in growth rates is related to species, crown position, diameter class, elevation (and simultaneously climate), and topographic position.

STUDY AREAS

The study areas were in the Luquillo Mountains of eastern Puerto Rico at latitude 18° N, longitude 66° W (fig. 1). The highest peak in these mountains, 1,076 m, is within 8 km of the ocean, and the abrupt elevational gradients cause dramatic changes in physical environment. Temperature and evapotranspiration decrease, and rainfall, relative humidity, and wind velocity all increase with altitude (Wadsworth 1951, Briscoe 1966, Weaver, Byer, and Bruck 1973). Soils range from organic mucks and calcereous sands in coastal zones through alluvial deposits in floodplains and acid clays in the mountains. Topography becomes increasingly dissected with elevation; and on the summits, aspect and slope are important determinants of vegetative growth forms. Diameters, tree heights, numbers of species, forest complexity, number of strata, all diminish with elevation within the forest (Wadsworth 1951, White 1963).

As a result of the sudden orographic uplift and cooling of the prevailing northeasterly trade winds, precipitation is nearly three times greater in the mountains than on the adjacent coast. Because of the frequent cloud cover over the mountains, total incoming solar radiation measured on El Yunque Peak (elevation 1,059 m) averages only 60 percent of that recorded at Cape San Juan on the coast (Briscoe 1966). At the base of the mountains, the mean annual temperature is about 26° C and the rainfall averages 1,700 to 2,050 mm annually; at the summits, the mean annual temperature is 19° C and 5,080 mm of rainfall have been measured (Wadsworth 1951). The mean annual temperature and precipitation for the study areas are intermediate between these extremes (table 1).

Once the ascent begins within the Caribbean National Forest, the following forest types (Beard 1944) are encountered: (1) lower montane rain forest ranging from the forest border through 600 m; (2) upper montane rain forest dominated by *Cyrilla racemiflora* L., *Micropholis garciniaefolia* Pierre, and *Micropholis chrysophylloides* Pierre, ranging from 600 m through 900 m (3) palm brake dominated by *Prestoea montana* (R. Grah.) Nichols, common on steep slopes and arroyos above 600 m; and finally, (4) dwarf forest, a bryophyte-laden, diminished vegetative type found on summits and ridges above 850–900 m.

The three study sites were in the lower montane rain forest. In Puerto Rico, this general classification corresponds to the tabonuco forest type, named for the dominant tree, *Dacryodes excelsa* Vahl., which can account for 30 percent of the basal area and more than half the timber volume in old-growth stands (Wadsworth 1953). Other tree species characteristic of this type include *Sloanea berteriana* Choisy, *Buchenavia capitata* (Vahl) Eichl., and *Manilkara bidentata* (A. DC.) Chev. in
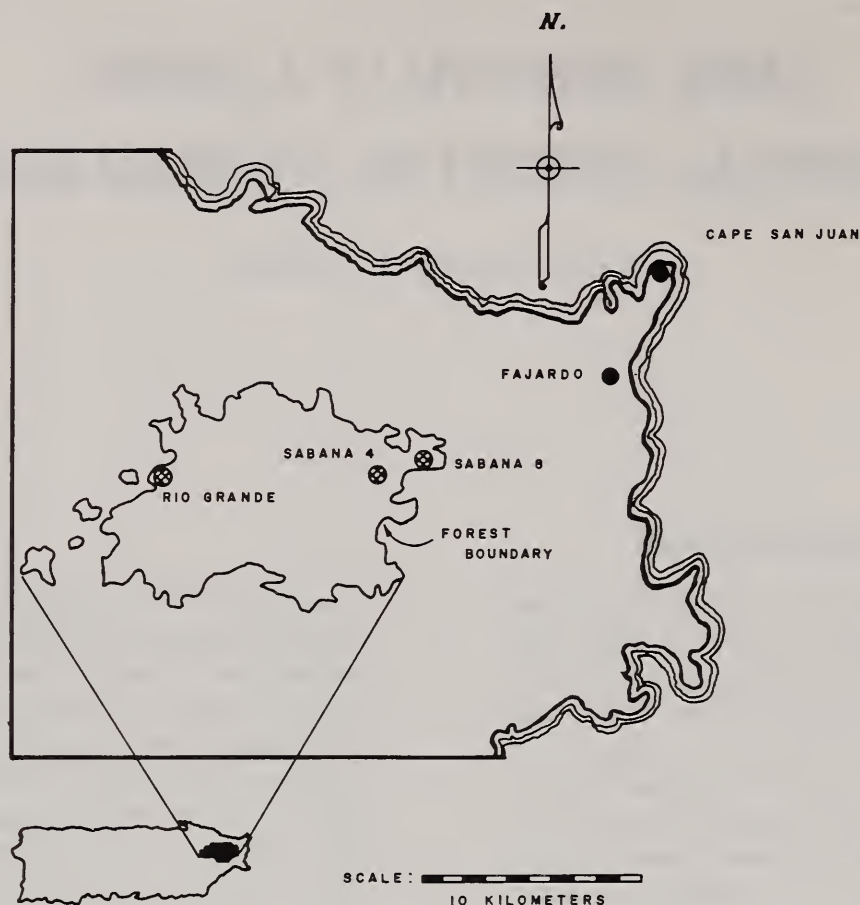
Figure 1. Location of Caribbean National Forest in Puerto Rico and location of study sites within the Forest.

the mature forest, and *Cecropia peltata* L. and *Didymopanax morototoni* (Aubl.) Decne. & Planch. in the secondary forest. Between 150 and 200 tree species are found in this forest type (Wadsworth 1947, 1951, 1953; Ewel and Whitmore 1973), most of which never attain dominance. The 18 tree species selected for study have potential commercial value and are common overstory species. The species, their important characteristics, and their distributions are listed in table 2.

According to Wadsworth (1953), the tabonuco type is found on 10,000 ha in Puerto Rico and is considered the climax vegetation on one-third of the land surface. Old-growth stands have two or three vegetative strata, a dense evergreen overstory at 30 to 35 m, abundant woody vines, epiphytes, and arborescent ferns. Shrubs and herbs are uncommon. Fewer than 400 ha of old-growth forest now exist in Puerto Rico; so most of this forest type consists of secondary stands with fewer species, simpler structure, and less biomass.

Study sites (table 1) include Sabana 8, an 80-ha tract of secondary forest located on the windward side of the mountains. It has the warmest and driest climate among the sites. Sabana 4, a mature stand of 129 ha, is also on the windward side of the mountains, receives the most precipitation, and is the most humid. Río Grande, a 40-ha secondary stand located on the leeside, is slightly drier than sites at similar elevations on the windward. Here on the leeside, 80 percent relative humidity is equalled or exceeded only 39 percent of the time, compared to 53 and 63 percent of the time for Sabana 8 and Sabana 4, (table 1). The deep acid clay soils are similar on all three sites, although microsite differences within each area are substantial.

Land-use varied among the three study sites. Sabana 8 is the most amenable to cultivation, and almost all of it was farmed at one time. A cover-type map made when the tract was purchased in 1947 indicates heavy brush with saplings at the lower elevations and "small and large poles" at the upper elevations. There is no record of extensive cultivation in the Río Grande tract, but a 1934 map shows pasture land in the lowest elevations, cutover forest at the intermediate elevations, and slope and sierra palm forest at the highest elevations. Additional tree harvest occurred in this tract between 1934 and 1957 when this study began. In contrast, Sabana 4 is a mature forest that has never been cultivated or used as pasture.

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Table 1.--A comparison of climatic, physiographic, soil, and vegetative features of the three study areas[1,2]

Parameter	Study sites		
	Sabana 8	Río Grande	Sabana 4
Mean annual temperature, °C	23	22	22
Mean relative humidty, %	75	76	79
Percent of hours when relative humidity is at or above			
80%	53	39	63
70%	74	68	80
60%	85	89	93
50%	96	99	99
40%	99	99	99
Precipitation, mm	2290	3300	3560
Aspect	north	west	east
Elevation.m above sea level	180-360	420-600	210-600
Soils	deep acid clay	deep acid clay	deep acid clay
Character of forest	cutover or secondary	cutover or secondary	mature

[1] Sources: Work Plan – Pilot Management in the Luquillo Experimental Forest (on file the Institute of Tropical Forestry); Briscoe (1966).

[2] Records for climatic data are from late 1958 through 1962.

METHODS

This study was pursued within the general framework of a pilot management project designed to increase forest productivity by eliminating the poorest growing species and providing ample growing space for select trees.

In 1957 about 100 plots 0.08 ha (1/5 acre) in size were established in a systematic fashion within each study area. Data recorded for each plot included: topographic position (i.e., bottom, lower slope, upper slope, ridge); species, diameter at breast height (dbh), and merchantable height of all trees >1.5 cm dbh. Within each plot, crop trees were identified and tagged; culls were marked for removal. Originally, it was intended that the secondary stands be thinned every 5 years to assure canopy freedom for crop trees. However, the treatment was applied only once at the beginning of the experiment. Sabana 4 was never treated but cannot be considered a control because of the climax nature of the forest.

In 1975 we reexamined the plots to determine the long-term growth rates. At Sabana 4 and Río Grande, 40 of the original plots were selected in proportion to their relative abundance within each topographic classification and surveyed. At Sabana 8 all plots were studied. On each plot, living crop trees were identified; and their dbh and mean annual increments in diameter and basal area were

determined. Growth is termed periodic annual increment (PAI) since means are based on a temporal segment of a tree's life and not on its entire life as implied by the term mean annual growth (Bruce and Schumacker 1950).

Data were analyzed with one-way ANOVA's and multiple range tests if significant differences were found with ANOVA. Tests of significance are reported at the 95 percent probability level unless stated otherwise.

RESULTS

Comparisons Among Species

Annual diameter increment (PAI) ranged from a mean of 0.25 cm for old-growth *Dacryodes* in Sabana 4 to 0.81 cm for *Guarea* in Sabana 8 (table 3). Maximum increments in excess of 1.00 cm were recorded for individuals of most species; the highest was for a *Buchenavia* tree. Twenty-seven trees however, had no measurable increment and many had only a few mm's of increment from 1957 to 1975.

Although the PAI for most species ranged between 0.30 and 0.60 cm, significant differences were found among species within each area: Sabana 8, $F = 5.224$, $df = 13, 269$, $P<0.01$; Río Grande, $F = 3.367$, $df = 16, 396$, $P<0.01$; Sabana 4, $F = 17.395$, $df = 19, 1298$, $P<0.01$. Among the prominent species at Sabana 8, *Tabebuia* grew significantly slower than all other species except *Didymopanax* (fig. 2). The group near the median, *Inga,*

Table 2.—Character and range of tree species in this study[1]

Species	Successional character	Maximum size Height (m)	Maximum size Dbh (cm)	Range
	Early secondary			
Cecropia peltata		21	60	West Indies; Mexico to Costa Rica. Colombia, Venezuela, and Guianas
Didymopanax morototoni		18	45	Widespread in the wet forests of tropical America
	Secondary			
Alchornea latifolia		9 – 15	45	Cuba, Jamaica, Hispaniola, Puerto Rico; also southern Mexico to Panama
Byrsonima coriacea		9 – 18	30 – 45	West Indies; Guianas to Colombia and Panama, south to Peru, Bolivia and Brazil
Inga laurina		15 – 21	45	West Indies; Western Mexico, Guatemala to Panama
Linociera domingensis		18	60	Cuba, Jamaica, Hispaniola, Puerto Rico, also Belize and Guatemala
Nectandra sintensisii		18	35	Puerto Rico
Ocotea leucoxylon		15	30	West Indies
Ormosia krugii		9 – 18	60	Hispaniola, Puerto Rico, Guadeloupe, Dominica
Tabebuia heterophylla		18	45	Hispaniola, Puerto Rico, Lesser Antilles
Zanthoxylum martinicense		6 – 12	45	Puerto Rico and Virgin Islands
	Primary			
Matayba domingensis		9 – 18	45	Cuba, Hispaniola, Puerto Rico
Homalium racemosum		21	60	West Indies, Mexico to Venezuela, Surinam, and northern Brazil
Guarea trichilioides		12 – 23	30 – 90	Greater Antilles; Costa Rica to Panama, south to Argentina and Brazil
Buchenavia capitata		18 – 24	60 – 120	West Indies; Panama and South America from Venezuela to Brazil and Bolivia
Dacryodes excelsa		30	90 – 150	Puerto Rico and Lesser Antilles
Manilkara bidentata		30	120	Hispaniola, Puerto Rico, Lesser Antilles; northern South America
Sloanea berteriana		30	60 – 90	Hispaniola, Puerto Rico, Lesser Antilles

[1] Source: Little and Wadsworth (1964)

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Byrsonima, Ormosia, Cecropia, Matayba, Manil-kara, and *Homalium,* did not differ in their rate of increment. The fastest growers, *Buchenavia, Guarea, Dacryodes,* and *Zanthoxylum,* differed significantly from only the four or five slowest growing species. At Río Grande only the fastest and slowest growers were significantly different (fig. 3). For example, *Sloanea* differed only from *Manil-kara* and *Buchenavia.* At Sabana 4 (fig. 4), only the slow-growing *Dacryodes* differed from other species. Its growth rate was significantly less than those for all other species except *Linociera.*

Reliability of the estimated means, as measured by the width of the confidence intervals, decreased with increasing rates of estimated diameter growth (figs. 2--4). This trend is partially attributable to decreasing sample size; faster-growing species were minor components of the stands and thus were sampled less frequently. In addition, the coefficient of variation for growth rates was high for all species (table 3), averaging between 55 and 60 percent for the three study areas.

When growth is expressed in terms of basal area (BA) increment, tree size as well as diameter growth becomes a factor. Because large trees of *Buchenavia* were capable of fast growth, this species had the highest rates of BA increment (table 3). Despite the preponderance of large size classes of *Dacryodes* in Sabana 4, mean BA increment was low because of the extremely low diameter increments recorded for the mature individuals of this species. The prominent tree in Sabana 8, *Tabebuia,* had the lowest mean BA increment because of both small tree size and slow diameter growth.

Growth Related to Crown Class

Growth was significantly and positively cor-related with an increase in crown dominance within the canopy (table 4). *Cecropia, Didymo-panax,* and *Dacryodes* were exceptions to this general pattern. *Cecropia* and *Didymopanax* are pioneering species intolerant of shade, and in both, PAI was comparable among codominant, inter-mediate, and suppressed individuals. Apparently these species require a dominant position before they can show improved growth. In contrast, growth rates for the shade-tolerant *Dacryodes* were not affected by position in the canopy unless a tree was suppressed.

Growth Related to Initial Diameter Class

When mean growth rates were plotted by initial (1957) diameter class (fig. 5), two trends were evident. Growth rates for *Alchornea, Ocotea,* and *Tabebuia* increased with increasing diameter class (fig. 5); big trees grew faster, perhaps because of a more favorable competitive position within the canopy. For the other species plotted, growth rates remained about the same regardless of diameter class.

Growth rates for *Didymopanax* and *Dacryodes* were remarkably uniform and appear to be inde-pendent of diameter class for the diameter range measured in this study (fig. 5). Caution must be used with *Didymopanax,* however, because of the long measurement interval and the possibility of short but rapid spurts of growth. Additional measurements of shorter duration on young trees are necessary for both *Didymopanax* and *Cecropia.*

Growth rates for *Inga,* though strongly correlat-ed with crown class (table 4), were apparently not related to diameter class (fig. 5). However, few measurements in the large diameter classes were available; so the graph may not tell the full story. When diameter increment was compared to initial diameter for all individuals of this species, a weak but significant correlation was found ($r = 0.23$, $p < 0.05$, $n = 148$).

Growth Comparisons Among Topographic Positions

Based on plot means, differences in PAI among topographic positions were not striking. Signifi-cant differences were found in only one of the three sites, Sabana 8 (table 5). At this location, the growth rates were highest in the bottomland, inter-mediate on ridge sites, and lowest on the slopes.

Some differences in growth rates among topo-graphic positions were correlated with differences in species composition. For example, the slow-growing *Tabebuia* predominated on slopes in Sabana 8, and it was the slopes that had the lowest growth rates in that area. The low growth rates recorded for ridge plots in Sabana 4 can be attri-buted to the dominance of slow-growing individuals of *Dacryodes.*

Growth Comparisons by Elevation

In the initial comparison, individuals from plots at the lowest elevations were compared to indi-viduals from plots at the highest elevations within each study area but without regard to topographic positions, species, or diameter class. Analysis showed significant trends only in the case of Sabana '8, where the elevational gradient is from 180 to 360 m (table 6). The greatest range in elevation within a study site was 210 to 600 m for Sabana 4, yet the differences in PAI for these extremes were not significant. Replication in Sabana 4, however, was less than half of that on the Sabana 8 site (table 6).

A second comparison, among individuals from high and low elevations and by topographic posi-tion but for all species, diameter classes, and study
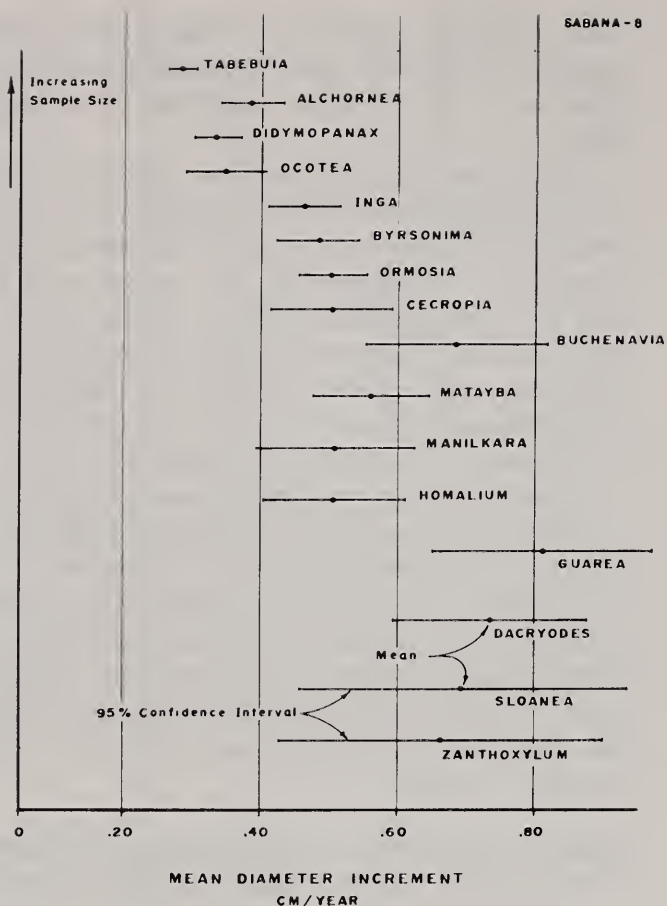
Increasing Sample Size

TABEBUIA
ALCHORNEA
DIDYMOPANAX
OCOTEA
INGA
BYRSONIMA
ORMOSIA
CECROPIA
BUCHENAVIA
MATAYBA
MANILKARA
HOMALIUM
GUAREA
DACRYODES
Mean
SLOANEA
95% Confidence Interval
ZANTHOXYLUM

0   .20   .40   .60   .80

MEAN DIAMETER INCREMENT
CM/YEAR

Figure 2. Mean diameter increment (cm) and 95% confidence intervals for species in Sabana 8.

Increasing Sample Size

DACRYODES
SLOANEA
CECROPIA
INGA
DIDYMOPANAX
ALCHORNEA
Mean
MATAYBA
95% Confidence Interval
LINOCIERA

0   .20   .40   .60   .80

MEAN DIAMETER INCREMENT
CM/YEAR
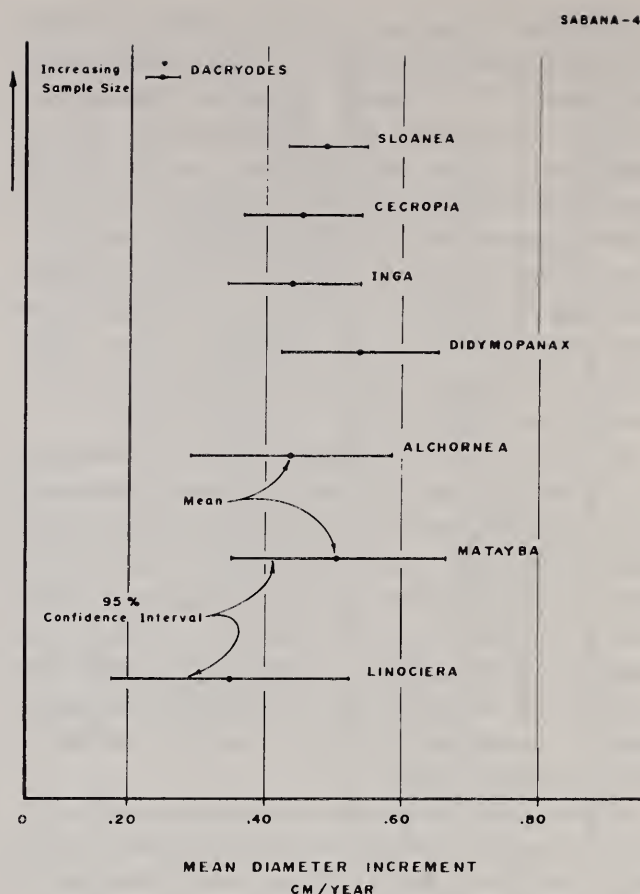
Figure 4. Mean diameter increment (cm) and 95% confidence intervals for species in Sabana 4.

Increasing Sample Size

DACRYODES
MATAYBA
TABEBUIA
CECROPIA
DIDYMOPANAX
MANILKARA
HOMALIUM
ORMOSIA
SLOANEA
LINOCIERA
Mean
OCOTEA
95% Confidence Interval
INGA
BUCHENAVIA

0   .20   .40   .60   .80
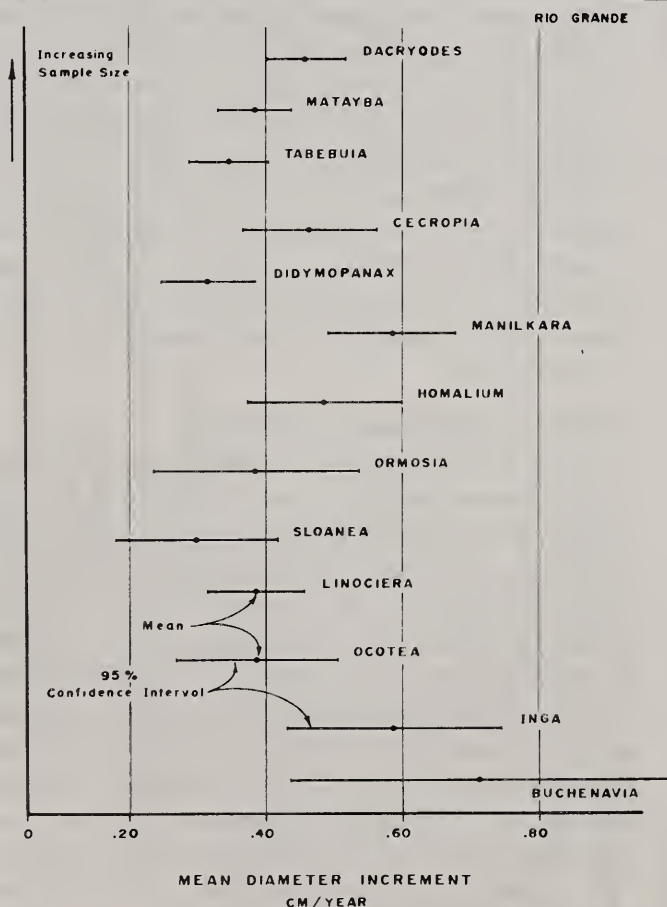
MEAN DIAMETER INCREMENT
CM/YEAR

Figure 3. Mean diameter increment (cm) and 95% confidence intervals for species in Rio Grande.

areas, showed significant trends only for ridge-top sites. Individuals growing on ridges at lower elevations grew significantly faster than individuals growing on ridge sites at higher elevations (table 7).

Comparison of PAI by species with adequate replication (>10 individuals), on both high and low plots within research sites, indicated significant differences in two of five cases (table 8). *Didymopanax* showed slower growth at lower elevations; *Tabebuia* at higher elevations.

Growth Comparisons Among Areas

Mean diameter increment differed slightly among areas, ranging from 0.38 cm/yr for Sabana 4 to 0.42 mm/yr for Río Grande (table 9). Although Sabana 4 had the lowest rate of diameter growth, it had the highest BA growth because of the large trees on the site (table 9).

Differences in averages among study areas could be attributed mainly to individual species. In Sabana 8 and Sabana 4, the slowest growing species happened to be the most prominent. Thirty-three percent of the stems in Sabana 8 were *Tabebuia* and it averaged only 0.28 cm/yr PAI. This species is the first to invade old-fields and it is likely that it invaded a depleted site following abandonment of agriculture on Sabana 8. *Dacryodes* accounted for 43 percent of the total stems in Sabana 4 and

Table 3. Mean dbh (1975), annual diameter increment (1957-1975) and measures of dispersion, mean annual basal area increment, and sample size for species in three study areas

Species	Mean dbh 1975	Diameter increment Mean	Diameter increment Range	Diameter increment Coefficient of variation	Mean BA increment	Number observed
	cm	----------cm/yr----------		%	cm^2/yr	
Sabana 8						
Alchornea latifolia	24.3	0.38	0.0-1.45	67.9	14.6	199
Buchenavia capitata	35.8	0.68	0.0-1.83	58.9	34.3	30
Byrsonima coriacea	21.7	0.48	0.02-1.02	45.9	14.1	61
Cecropia peltata	31.7	0.51	0.08-1.55	64.5	22.6	49
Dacryodes excelsa	30.1	0.74	0.48-1.32	33.5	28.2	11
Didymopanax morototoni	23.3	0.33	0.0-1.09	71.5	11.1	134
Guarea trichilioides	32.4	0.81	0.13-1.35	46.8	33.2	18
Homalium racemosum	23.3	0.51	0.15-0.91	47.1	15.6	18
Inga laurina	22.8	0.46	0.0-1.17	54.9	15.1	114
Manilkara bidentata	26.3	0.51	0.02-1.12	60.3	22.3	22
Matayba domingensis	24.6	0.56	0.0-1.02	44.0	18.2	24
Nectandra sintenisii	18.3	0.35	0.0-0.65	60.1	9.0	6
Ocotea leucoxylon	19.8	0.35	0.0-1.27	76.6	10.6	115
Ormosia krugii	24.2	0.51	0.0-1.14	44.2	17.2	59
Sloanea berteriana	28.9	0.69	0.15-1.22	54.0	27.7	8
Tabebuia heterophylla	19.0	0.28	0.0-1.04	69.5	8.1	459
Zanthoxylum martinicense	25.1	0.66	0.38-1.14	44.1	21.0	5
Río Grande						
Alchornea latifolia	22.2	0.33	0.02-0.68	69.3	11.7	9
Buchenavia capitata	35.9	0.71	0.08-1.57	74.3	38.4	11
Cecropia peltata	27.0	0.46	0.02-1.09	69.8	16.7	35
Dacryodes excelsa	30.6	0.46	0.0-1.07	54.0	19.1	79
Didymopanax morototoni	23.6	0.31	0.0-0.89	77.1	10.6	36
Homalium racemosum	28.5	0.48	0.10-1.02	50.9	20.1	18
Inga laurina	39.9	0.58	0.18-0.81	42.8	30.7	8
Linociera domingensis	21.2	0.38	0.18-0.63	34.4	12.0	15
Manilkara bidentata	27.8	0.58	0.08-1.14	46.4	23.7	27
Matayba domingensis	21.9	0.38	0.02-1.17	55.1	11.9	63
Ocotea leucoxylon	25.1	0.38	0.05-1.12	74.3	12.9	13
Ormosia krugii	30.5	0.38	0.05-1.32	78.6	17.3	18
Sloanea berteriana	22.3	0.30	0.02-0.86	83.0	10.3	17
Tabebuia heterophylla	22.9	0.35	0.0-0.76	59.7	12.0	55
Sabana 4						
Alchornea latifolia	27.7	0.43	0.02-1.07	73.9	18.7	17
Cecropia peltata	29.1	0.46	0.05-1.24	62.4	17.6	33
Dacryodes excelsa	34.9	0.25	0.0-0.81	63.9	13.4	117
Didymopanax morototoni	31.8	0.53	0.08-1.35	59.3	23.4	23
Inga laurina	26.0	0.43	0.0-0.99	68.1	16.6	28
Linociera domingensis	18.1	0.35	0.13-0.63	59.2	9.4	5
Matayba domingensis	25.8	0.51	0.33-0.74	32.3	16.2	9
Sloanea berteriana	26.9	0.48	0.01-1.35	47.4	19.1	41

Table 4.—ANOVA of mean annual diameter increment among crown classes[1]

Succesional status/species	Area	Mean annual diameter increment				F ratio[2]	df	SNK test[3]
		D	CD	I	S			
		-----cm/yr-----						
Early secondary								
Cecropia peltata	Sabana 8	0.571	0.402	0.389	0.324	1.415 n.s.	3,44	
Didymopanax morototoni	Sabana 8	0.448	0.328	0.253	0.187	6.190 **	3,128	D>CD=I=S
Late secondary								
Alchornea latifolia	Sabana 8	0.633	0.534	0.367	0.110	22.739 **	3,189	D>CD>I>S
Inga laurina	Sabana 8	0.768	0.524	0.326	0.189	27.857 **	3,108	D>CD>I>S
Ocotea leucoxylon	Sabana 8	0.719	0.519	0.380	0.163	17.179 **	3,106	D>CD>I>S
Tabebuia heterophylla	Sabana 8	0.380	0.320	0.210	0.093	36.469 **	3,434	D>CD>I>S
Tabebuia heterphylla	Río Grande	0.465	0.397	0.250	0.093	7.493 **	3,45	D>CD>I>S
Early primary								
Matayba domingensis	Río Grande	0.303	0.469	0.378	0.172	5.574 **	3,59	D=I
Late primary								
Dacryodes excelsa	Sabana 4	0.292	0.264	0.286	0.183	0.939 n.s.	3,111	C>I>S
Sloanea berteriana	Sabana 4	0.973	0.560	0.468	0.234	12.310 **	3,35	D>CD>I>S

1/ Only species with sufficient replications in each crown class were included.

2/ n.s. P>0.05
   ** P<0.01

3/ Multiple comparisons among means based on the Student-Newman-Keuls test; D>CD indicates that the mean diameter increment for dominant trees was significantly greater than that for codominant trees; etc.

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most were mature individuals with minimal diameter increments ($\bar{x}$ = 0.25 cm/yr). Thus a slightly different perspective is gained from the comparison of unweighted averages as compared to the weighted averages in table 9. For Sabana 8, Río Grande, and Sabana 4, the (unweighted) average PAI's were 0.52, 0.43, and 0.43 cm/yr, respectively.

It is also noteworthy that in Sabana 8, a secondary stand, *Buchenavia*, *Dacryodes*, *Guarea*, and *Sloanea*, all primary species, had above-average rates of diameter growth. It is possible that conditions in this secondary forest are now ideal for the rapid growth and development of primary species, and if their propagates were available in large quantities, a primary component would develop very rapidly. Also of interest is the fact that secondary species (i.e., *Cecropia* and *Didymopanax*) remain an important component of the mature stand at Sabana 4. Apparently the abundant rain and occasional high winds in combination with unstable soils and steep topography produce a constant niche in time and space for these secondary species.

DISCUSSION

Our data indicate that year-round growing conditions, warm temperatures, and abundant rainfall do not produce rapid rates of diameter increment in the tropical rain forests of the Luquillo Mountains. Our findings are supported by several earlier studies of tree growth within the lower montane rain forest of Puerto Rico (Wadsworth 1947, Murphy 1970), and similar studies elsewhere in the humid tropics (Keay 1961, Kira 1969, Bell 1971, Prince 1973, Whitmore 1974). Kira (1969) stated that the annual diameter increments for trees in the "stabilized rain forest" rarely exceeds 1 cm/yr, a figure that corresponds to the maximum increment for most species measured in this study. These data support Leslie's (1976) contention that low rates of commercial increment are typical of moist tropical forests and these low rates represent a major problem in the management of natural forests.

This skepticism seems to contradict the belief that moist tropical forests are among the most
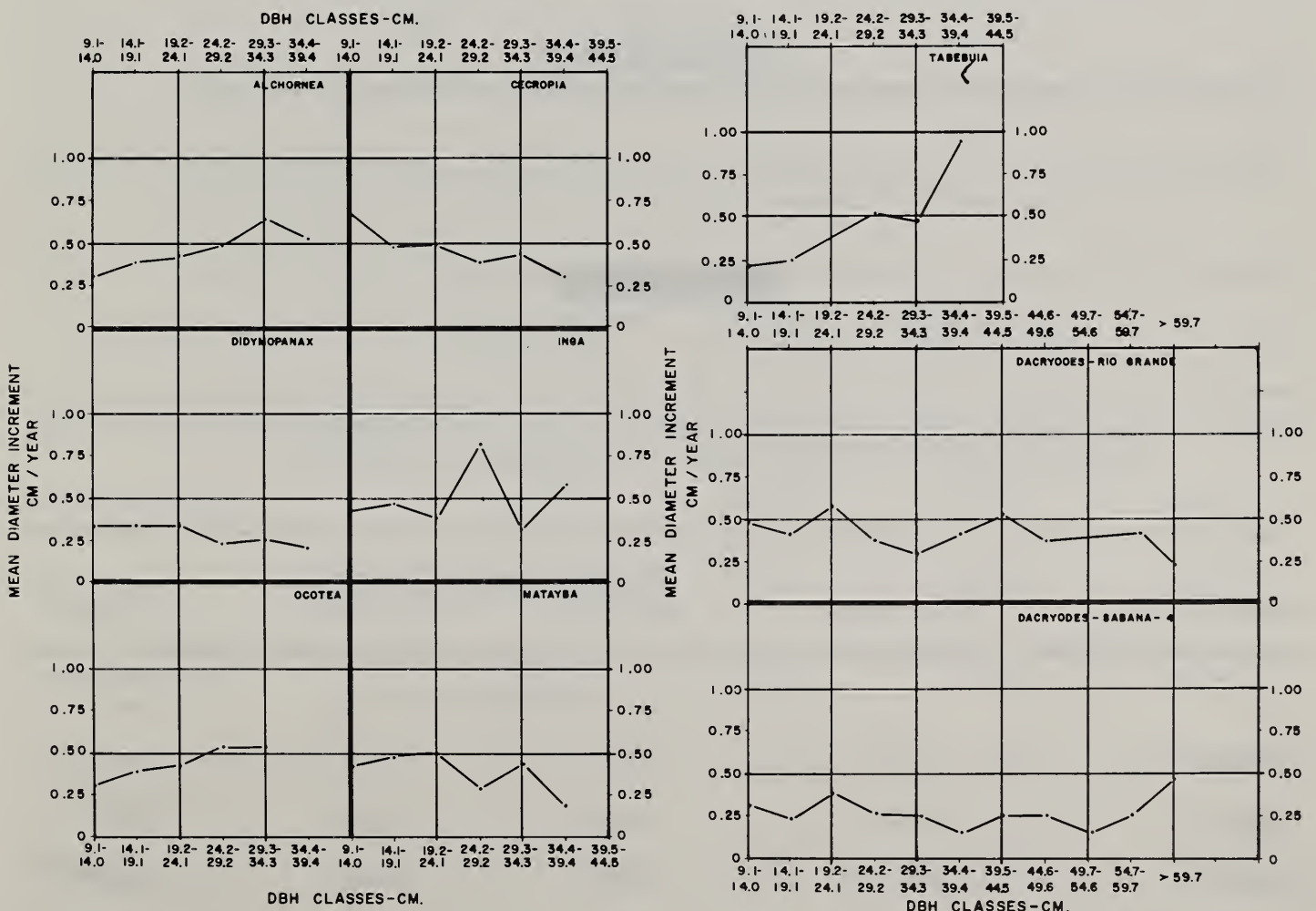

Figure 5. Mean diameter increment plotted by diameter class at time of initial measurement. Only species with large samples (>100) were included. Data for a species were pooled if no significant differences were found in diameter increments among study areas. The data utilized are *Alchornea* and *Tabebuia*, Sabana 8; *Cecropia* and *Matayba*, Sabana 8, Rio Grande, Sabana 4; *Didymopanax* and *Ocotea*, Sabana 8, Rio Grande; *Inga*, Sabana 8, Sabana 4; *Dacryodes*, Rio Grande, Sabana 4.

Table 5.--Mean annual diameter increment for plots at different topographic
positions within each study area

Topographic position		Sabana 8	Río Grande	Sabana 4
		------------cm/yr-------------		
Bottomland	Mean (cm/yr)	0.529	0.431	0.367
	N	13	6	6
Lower slope	Mean	0.392	0.408	0.421
	N	29	12	12
Upper slope	Mean	0.391	0.417	0.448
	N	58	18	17
Ridge	Mean	0.432	0.461	0.334
	N	5	4	4
	ANOVA	$F=5.299(df=3,101)$	$F=0.221(3,36)$	$F=0.633(3,36)$
		$P<0.01$	n.s.	n.s.

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Table 6.--Comparison of mean annual increments on low- and high-elevation plots within
research sites but without regard to topography or species

Research site	Observation	Periodic annual increment		F ratio
		Low plots	High plots	
		---------cm/yr----------		
Río Grande 3	74/79	0.477	0.477	0.43
Sabana 4	62/42	0.460	0.500	0.48
Sabana 8	105/148	0.450	0.404	1.62**[1]

[1] $P<0.01$

Table 7.—Comparison of mean annual increment of low- and high-elevation plots by topographic position but without regard to research site or species

Topographic position	Observations Low/High	Periodic annual increment		F Ratio
		Low plots	High plots	
	No.	----------cm/yr----------		
Bottomland	28/19	0.498	0.477	0.47
Lower slope	119/20	0.462	0.378	.1.50
Upper slope	87/200	0.429	0.444	0.16
Ridge	9/32	0.632	0.371	6.83**[1]

1/ ** P < 0.01

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Table 8.—Comparison of mean annual increment by species on low- and high-elevation plots within research sites but without regard to topography

Species (Site)	Observations Low/High	Periodic annual increment		F ratio
		Low plots	High plots	
	No.	-------cm/yr--------		
Alchornea latifolia (Sabana 8)	12/48	0.343	0.391	0.27
Inga laurina (Sabana 8)	18/20	0.467	0.477	0.03
Dacryodes excelsa (Sabana 4)	17/10	0.274	0.282	0.00
Didymopanax morototoni (Sabana 8)	22/17	0.188	0.386	10.77**[1]
Tabebuia heterophylla (Sabana 8)	18/25	0.485	0.234	18.42**

1/ ** P < 0.01

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Table 9.--Average growth for individual trees by study area[1]

Study area	Sample size	PAI	BA increment
		cm/year	m^2/year
Sabana 8	1384	0.391	0.188
Río Grande	404	0.419	0.231
Sabana 4	273	0.376	0.234

[1] Means weighted by number of sample individuals for each species.

productive of the earth's ecosystems (Becking 1962, Rodin and Bazilevich 1967, 1968, Murphy 1975, Olson 1975, Rodin et al. 1975). Admittedly, extraordinary rates of growth have been reported for some tropical and subtropical species. However, such rates are almost always associated with young secondary species or exotic species in plantations, often with fertilization, and many times in biotic and climatic provenances other than the rain forest.

For example, eucalyptus *(E. grandis)* introduced to eastern Brazil grew 28 cm in dbh and 29 m in height in only 6 years (Rance 1976). Johnson (1976) found that plantations of *Pinus caribaea, Gmelina arborea*, and *Albizia falcataria* produced 10 to 20 times more volume than indigenous tropical forests.

It is also recognized that the measure of growth utilized in this study (commercial or economic increment) is not necessarily a good indicator of biological growth measured as primary production. But there is additional evidence in terms of primary production to justify caution in characterizing growth patterns in moist tropical forest.

In comparing patterns of primary production, Jordan (1972) concluded that rates of woody production are "similar in many intermediate aged stands on mesic sites regardless of latitude, but rate of leaf and litter production is slightly higher in the tropics." Dawkins (1963) believes that the general limit of woody production for most indigenous tropical forests is 10 dry-weight tons per hectare, a figure that approaches the averages cited for temperate forests. If primary production in the moist tropics is indeed higher than in the temperate zone, the differences may be due to nonwoody production.

Physiological factors may also reduce net production in tropical forests. Here most features add up to a plant physiology geared to efficient use of resources and large expenditures of energy for maintenance at the expense of rapid growth (Odum 1962, Odum and Jordan 1970, Smith 1970). This efficiency results in the ability to compete in an environment of intense competition.

The fact remains that tropical forests represent a vast array of biotic and abiotic entities, with information about the long-term capability to produce organic matter available for only a few of these ecosystems. The limited data seem to indicate a skewed distribution in growth rates (both biological and commercial) toward the lower rates, but with a long tail of high rates. If such a distribution is the case, the median rate of production is a better measure of the central location within the distribution than is the mean. Median values would also be less than the mean rates of forest production published for the moist tropics.

Surprisingly, the slowest growing species in our study were *Cecropia* and *Didymopanax*; both are pioneer species and supposedly rapid growers. For example, young *Cecropia* is reported to grow 5 to 7.5 cm in diameter per year (Little and Wadsworth 1964). We recorded much slower growth rates for *Cecropia*, even in Sabana 8, a young stand where rapid growth of early secondary species would be expected. Possibly the period of rapid diameter growth had subsided before the initial measurement in 1957, or the period of remeasurement in this study was too long to detect a short but rapid spurt of diameter growth. Both species have strong apical dominance and establish a competitive

position within the canopy by rapid vertical growth. Once these species reach the upper stratum, it is likely that the rapid growth rates are not sustained, and over a long measurement period such as in this study, the average rates are low.

As reported elsewhere for tropical forests (Keay 1961, Baur 1964, Mervart 1970, Whitmore 1974), individual trees in the Luquillo Forest varied widely in their growth rates. In Luquillo, there were cases where apparently healthy trees had no measurable diameter growth during the 18-year period, but nearby trees of the same species, similar size, and physiognomy approached the maximum rates for the species.

The magnitude of this variation and the limitations of simple correlations for a multivariate set of relationships made it difficult to ascribe growth differences to the various factors. A strong correlation was found between crown position and productive capacity, and presumedly crown position is a good indicator of growth potential in this rain forest. Logically related to competitive position within the canopy was the trend of increasing growth rates with increasing tree size established for several species. Other factors accounted for little of the variability among rates. Significant differences among species were found only for the very slowest and fastest growers. Growth rates are known to differ with elevation, but elevation explained little of the total variability in our study, either because the gradients were not sufficient to produce consistent differences or because the sampling design was inadequate to detect differences. Differences among topographic positions were not consistent. Microtopography is suspected to be responsible for growth differences (Wadsworth 1970), but only macro-differences could be assessed by our topographic parameters.

This lack of success in identifying factors responsible for growth differences is common to the literature and it is reflected in a poor understanding of growth processes in the tropics. Nevertheless, growth rates presented here provide a measure of the long-term performance for species in the Luquillo Forest and if the maximum rates recorded for each species in table 3 are indicative of potential growth rates under ideal conditions, proper cultural treatments should significantly increase the mean rates.

The stimulation of growth rates will be an important goal in any silvicultural program in these forests; but in the mountainous terrain of the Luquillo Forest, watershed protection is also paramount. It is known from work in Africa that only the boldest treatments are likely to increase growth rates significantly (Dawkins 1958). So the challenge becomes that of balancing the need to protect soils and maintain a vegetative cover with the need to drastically modify the stand in order to provide ample growth space for select trees.

❦

SUMMARY

Measurements taken in 1957 and again in 1975 indicate slow rates of diameter growth for trees in a moist tropical forest of Puerto Rico. Mean diameter increments (PAI's) for species typically ranged between 0.30 and 0.60 cm/yr. The maximum PAI for the sample population (n=2,061) was only 1.83 cm/yr. Significant differences in growth rates were found among species and crown classes. The mean rates for individuals in the secondary stands varied little from the mean for the primary stand.

RESUMEN

Las medidas tomadas en el 1957 y luego en el 1975 indican un crecimiento de diámetro lento en los árboles de un bosque húmedo tropical en Puerto Rico. El crecimiento del diámetro medio (IAP) para las especies fluctuó típicamente entre 0.30 y 0.60 cm/año. El IAP máximo para la población de muestra (n=2,061) fue solamente 1.83 cm/año. Se hallaron diferencias significativas en la velocidad de crecimiento entre las especies y las clases de copa. No hubo mucha variación entre la velocidad media para los árboles individuales en los rodales secundarios y la media del rodal primario.

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